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E. Nettleship Esq
with the writer's regards.

NOTE ON THE KNEE-JERK AND THE CORRELATION OF ACTION OF ANTAGONISTIC MUSCLES.

BY

C. S. SHERRINGTON, M.A., M.D.

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FURTHER NOTE ON THE CORRELATION OF ACTION OF ANTAGONISTIC MUSCLES.[1]

BY C. S. SHERRINGTON, M.A., M.D. F.R.S.

IN a previous communication[2] it was shown that physiological contraction, and even mere mechanical tension of the flexor muscles of the knee, exerts considerable physiological influence upon the activity of the antagonistic muscles, the extensors. For instance, the elicitation of the "jerk" from the extensors can be rendered impossible or difficult for a time by appropriate excitation of the flexors, and can, on the other hand, be much facilitated by flaccidity or paralysis of the latter.

In order to judge whether under these circumstances the briskness of the knee-jerk varies directly with the degree of tonus of the extensor muscles, the rapidity of onset of rigor mortis has been selected as a guide to the degree of tonus obtaining in them before death. The experiments of Brown-Séquard, Kölliker, and Hermann and his pupils, have discovered that section of the nerve of a muscle, even when performed very shortly before the death of the animal, considerably delays the time of onset of rigor mortis in the muscle. After control experiments which simply verified the statements by these observers, experiments were instituted on the influence of section of the motor spinal roots upon the time of onset of rigor mortis. The examination showed that a marked delay of onset of rigor mortis was thus produced. The delay seemed to be as considerable as after section of the entire muscular nerve. The effect of section of the posterior roots was next examinad, and found to be a marked retardation of the onset of the rigor; the retardation was greater if the spinal cord remained intact than if the cord were previously severed across in the region of the first lumbar segment. The effect of placing and keeping one of the hind limbs in the pose most favourable for elicitation of the jerk (knee flexed) and the other limb in the position in which the jerk is restrained (knee extended) was investigated, in every case after previous severance of the spinal cord at the first lumbar segment. It was found that upon the side on which the knee had been kept flexed the onset of rigor was delayed in the extensor muscles, whereas upon the opposite side, in which the knee had been kept extended, rigor was delayed in the flexors. This infers that the tonus of the extensors is heightened by excitation of the antagonistic set, and conversely.

The research was also extended to the examination of the mutual association of action of antagonistic muscles about other joints than the knee. It had been noticed in an earlier series of observations[3] that during excitation of the cortical areas of the hemisphere, when isolated movements of the

[1] Abstract of a paper communicated to the Royal Society.
[2] Sherrington, *Proceedings of the Royal Society*, February 1st, 1893.
[3] *Journal of Physiology*, vol. xiii, 1892.

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pollex and hallux are being initiated, the movement of response obtained is often reversed by section of the peripheral nerves supplying the muscles predominating in the movement obtained. Thus, for instance, flexion can, by section of the flexor nerve, be converted into extension or *vice versâ*. Sometimes, however, movement in the same sense, although diminished in force and extent, persists even after section of the motor nerve to the predominant group of an antagonistic pair, thus indicating that in some cases accompanying contraction of the one group of muscles there is concomitant inhibition of the antagonistic. This evidence of inhibition of one set of the synergetic muscular couple during the co-ordinate movement induced by cortical excitation is in the cases of the digits, hallux, and pollex comparatively infrequent, but it is quite usual in the case of ocular movements. By stretching or by exciting with tetanising currents the inferior oblique muscle of the eye, reflex movements in both eyes can be readily evoked, but these are of variable direction. When, the external rectus muscle of one eye (for example, of the left eye) having been put out of action, the frontal cortex of the right hemisphere is excited, the eyeballs, if previously directed to the right, revert both of them to the left—that is, the excitation which evokes contraction of the right internal rectus evokes also relaxation of the left internal rectus. Again, when the internal rectus has been put out of action—for example, in the left eye—excitation of the left frontal cortex produces, if the eyes have been previously directed to the left, an immediate movement of both eyeballs to the right, the left eye frequently rotating beyond the median primary position. Here the same excitation of the cortex which induces contraction of the right external rectus muscles induces synchronously a relaxation of the left internal rectus muscle.

These inhibitions of the contraction of one antagonist concurrent with augmentation of the contraction of its opponent are obtainable as well from appropriate areas of the occipital cortex as from areas in the "motor" region. Also there can be inhibited from the cortex not merely the "tonus," but the active contraction of ocular muscles. During volitional movements similar phenomena occur, but appear to be less obvious than during experimental excitation of the hemisphere with moderate currents. Although inhibition of contraction is apparently so common a factor in the mechanism of the mutual co-ordination of the antagonistic lateral straight muscles of the eyes, they yield occasionally good indication of the existence of synergetic contraction as well as synergetic relaxation. The mutual association of the two oblique muscles of the eye seems to be usually of the nature of concomitant contraction, not of contraction coupled with relaxation. On the other hand, the muscles which close and open the palpebral fissure appear to be altogether independent one of the other in action. In their case section of the particular peripheral nerve concerned in the movement is followed by total disappearance of the movement, and that without reversal. Although the cerebral cortex exercises inhibition apparently so usually in the field of innervation of the third nerve, the dilatation of the pupil readily produced by excitation of that portion of the cortex appeared whenever tested to be due to impulses discharged *viâ* the cervical sympathetic, and not to inhibition of the constriction exercised *viâ* the third nerve.

[*From the* PROCEEDINGS OF THE ROYAL SOCIETY, Vol. 52.]

"Note on the Knee-jerk and the Correlation of Action of Antagonistic Muscles." By C. S. SHERRINGTON, M.A., M.D. Communicated by Professor M. FOSTER, Sec. R.S. Received February 1, 1893.

(From the Physiological Laboratory, St. Thomas's Hospital.)

The muscular reaction known as the knee-jerk is notoriously affected by conditions obtaining in what is often described as a reflex arc, consisting of afferent and efferent paths, and a centre situate in the lumbar portion of the spinal cord. I recently* described experiments determining more particularly than hitherto the locality of the muscular and nervous mechanism on which the jerk depends. I showed that the muscular portion of this mechanism consists mainly

* 'Journal of Physiology,' vol. 13, p. 666.

of the *vastus internus* and part of the *crureus* divisions of the great quadriceps extensor muscle of the thigh. The *spinal centre* was found located in the 5th and 4th lumbar segments of the cord of the *Rhesus* Monkey (4th and 3rd lumbar of Man). The *efferent* path was found in the anterior roots of the 5th and 4th lumbar nerves, and was traceable along the anterior crural nerve into those of the muscular branches of that trunk which supply the above-mentioned portions of the quadriceps extensor max. The efferent side of the path corresponds accurately with the course of the motor nerve fibres to the muscles in question, and there is little reason to doubt that it consists of nothing more or less than of those motor fibres themselves. The *afferent* path was found to lie in the posterior root of the 5th lumbar of *Rhesus* (4th of Man, 6th of Cat), and was not usually demonstrable at all in the posterior root of the 4th lumbar, but a small portion of it may, perhaps, lie within that root.

The posterior root in which exists the afferent path on which the jerk is dependent receives afferent fibres from the obturator and anterior crural nerves, and from the external and internal popliteal nerves, and sometimes from the division of the great sciatic which may be called the hamstring nerve, because distributed to the hamstring muscles. Of the fibres entering the root from these various sources, those on which the "jerk" depends are not from any except the anterior crural nerve. Further, in the anterior crural nerve, they are those fibres of the nerve which issue from the vastus internus and crureus muscles. Thus the afferent fibres on which the jerk depends seem to arise within muscles, and from exactly those muscles, to which belong the efferent fibres with which the "jerk" is concerned.

The rapid abolition of the jerk produced by severing the posterior root of the 5th lumbar of *Rhesus* may conceivably be due less to mere interruption of an afferent path than to excitation of an afferent path by the "current of injury" set up in the injured fibres ("demarcation current") of it. This doubt has frequently been strengthened in my mind by the fact that section of one half the root often suffices to abolish the "jerk," although the remaining half can, when tested, still be shown able to conduct centripetal impulses from the skin; and further, by the fact that it appears immaterial whether the anterior or the posterior part of the posterior root be selected for the section. The "jerk" I have seen then abolished in a manner not obviously different from that in which section of the whole root abolishes it. Against such an explanation is, however, the permanence of the effect upon the "jerk" produced by section of the whole root, for the effect continues at least for many days. Regarding the permanence of the effect of section of half the root I have no observation.

I have repeated the observation substituting for severance other modes of destruction of the conductivity of the root. The root is a fairly long one, longer in the Monkey than in the Cat, and it is not difficult to apply reagents to it. I find the jerk immediately abolished by cooling the root to near the freezing point. To do this I pass under the posterior root, well lifted from the anterior, one end of a copper strip, the other end of which lies in an ice and salt mixture. The application of CO_2 vapour to the root has a similar effect, and on removing the vapour the "jerk" returns. The vapour I have applied through a thin-walled india-rubber tube, made to enclose the root. Cocain I have also applied, and found it abolish the jerk in about 70 secs., when used as a 1 per cent. solution in 0·6 per cent. sodium chloride solution. I place under the root, before applying the cocain, a thin strip of india-rubber sheeting, and apply the solution with a fine camel's-hair brush by painting on the filaments of the root.

There seems, therefore, no doubt that abolition of the jerk can be produced by lowering the conductivity of the fibres of this posterior root. Whatever the nature of these afferent fibres which thus come up from part of the quadriceps extensor of the thigh, and keep the "knee-jerk" going, facts show that they are less hardy under experimental interference than are those from the skin which carry centripetal impulses subserving tactile sensation. A very little interference with this posterior root abolishes the knee-jerk; a very great deal will often not obviously impair cutaneous reflexes elicited through it. To lift the posterior root by a thread passed under it will often suffice to interrupt the afferent fibres for "the jerk," but at the same time leaves the afferents of tactile sense not obviously impaired. Probably the former fibres are much the smaller and more delicate.

The irritation of this root, when cut, by its own demarcation current does not cause inhibition of the jerk. I have tried on three occasions to recover the "jerk," after its disappearance on section of this root, by electrical excitation of the central end of the divided root. The excitation, when too feeble to elicit any reflex contraction of the muscles, did not obviously influence the briskness of the jerk in either direction. The excitation very readily, however, causes contraction of the *hamstring* muscles, which so alters the position of the knee that the condition of the "jerk" can no longer be satisfactorily compared with what it was before.

Excitation of the central end of the divided hamstring nerve does at once abolish, or greatly reduce, the briskness of the "jerk." I have elsewhere* described a curious fact concerning the "jerk," namely, that it can be rendered brisk by section of afferent, or of

* 'Journ. of Physiol.,' *loc. cit.*

efferent, spinal roots immediately below that one on which the jerk itself depends. I added, with regard to it, "Its explanation appears to lie in the abolition of the tone of the hamstring muscles by section of the afferent roots belonging to them." I wish now to support, and somewhat enlarge, the explanation then offered.

Severance of the great sciatic trunk produces, as Tschiriew* has pointed out in the Cat, an increased briskness of the "jerk." This I find to depend scarcely at all, if indeed at all, on section of the external or internal popliteal divisions of the trunk, either singly or together; but to depend upon the cutting that portion of the trunk which is destined for the hamstring muscles—the portion referred to in my previous paper as "the hamstring nerve." In *Macacus* this "hamstring" division of the sciatic sends afferent fibres into the spinal cord by the posterior roots of the 8th, 7th, and 6th sub-thoracic nerves. In Cat, the 8th and 7th posterior roots are those in question. On severance of these afferent roots, the "tonus" of the hamstring muscles is broken, and the "jerk" becomes more brisk; sometimes there is a short interval of depression immediately succeeding the operation. The motor fibres of the hamstring muscles leave the cord by the anterior roots, correspondent with the above-mentioned posterior. Severance of these anterior roots causes immediate increase in the briskness of the jerk.

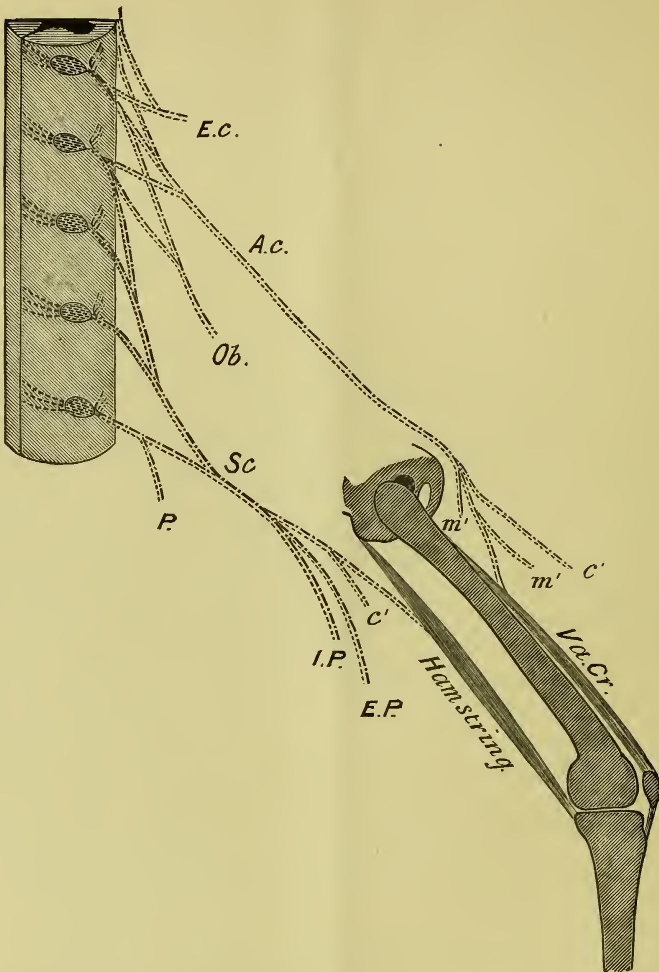
As to the manner in which the loss of tonus of the hamstring muscles gives rise to increase of the knee-jerk, two possibilities at once present themselves. One is purely mechanical; the other is of a physiological nature. The loss of tension accompanying the loss of "tone" will leave the leg more free to swing at the knee joint. It is for that reason that the posture of limb usually employed as the most favourable when the jerk is to be elicited is with the hamstrings relaxed and the leg at a right angle with the thigh. In this way the points of bony attachment of the hamstring muscles are approximated, and the knee can swing through a greater arc to that point at which it is cut short by the mechanical check of the flexor muscles passively tightened by the movement. The extensor movement during the "jerk" has, in this way, further scope before the hamstrings break it. As far as this explanation goes, the above-mentioned increase of the jerk would occur even if the hamstring muscles were replaced by india-rubber cords, the effect produced by severance of the hamstring nerve being equivalent to any arrangement which rendered those india-rubber cords less tight.

I should have considered this simple explanation sufficient had it not been for certain additional facts. During experiments on the effects of stimulating the motor spinal roots of the lumbo-sacral nerves there is much risk of being deceived by escape of the excit-

* 'Arch. f. Psych.,' vol. 8.

ing current to other motor roots besides the one to which the electrodes are applied. When stimulating the motor root of the 7th lumbar, I frequently observed contraction of the extensor muscles of the knee as well as of the flexors, and imagining that the phenomenon must be due to escape of the exciting current to the 5th lumbar root, I was accustomed to reduce the strength of the exciting current until the contraction of the extensors of the knee no longer occurred. To avoid this supposed escape of current, it was necessary to reduce the strength of stimulus sometimes to very slightly indeed above minimal efficiency for the motor fibres to which the electrodes were applied. The use of such weak currents has serious disadvantages, and was extremely embarrassing for the experiment. It was not until I had discarded a number of experiments on the ground of escape of current, that three points concerning the contraction of the extensor muscles produced by stimulating the motor nerve to the flexors attracted my attention. (1.) If for the excitation of the motor root to the flexors a series of induced currents are employed, succeeding each other at a rate slow enough to produce not perfect tetanisation, but tremulent contraction of the muscles, the contraction obtained in the extensor muscles coincidently was, nevertheless, perfectly steady and tetanic, although not vigorous. (2.) If the flexor muscles are severed from connexion with the knee joint, so that their contraction cannot affect the joint, and if the "knee-jerk" be elicited before, during, and after stimulation of the motor root to the flexor muscles, *during the excitation*, when those flexor muscles were contracting, the knee-jerk, brisk previously and brisk later, disappeared, or almost disappeared. (3.) If the sensory spinal roots belonging to the hamstring nerve are severed, the stimulation of a motor root to the hamstring muscles is no longer accompanied by contraction of the extensor muscles of the knee, even when strong stimulation is employed.

One next observed the effect on the extensors of the knee of excitation of the central end of the nerve to the hamstring muscles after that nerve had been ligated and cut through. It was found that excitation with currents just perceptible at the tip of the tongue causes immediate *disappearance* or diminution of the "knee-jerk." "Exaltation" of the jerk follows the depression by the excitation. If the excitation be continuously maintained for a time, the jerk tends to return in spite of the continuance of the stimulation. By use of stronger currents the extensors are immediately thrown into a tonic contraction, lasting so long as the stimulus is continued. The same effects on the knee-jerk, and on the activity of the extensor muscles, are elicited by exciting the central ends of the divided posterior roots of the 7th or 8th subthoracic nerve.



E.c. External cutaneous nerve trunk.
A.c. Anterior crural nerve trunk, with *c*, cutaneous, and *m'*, muscular, branches.
Ob. Obturator nerve-trunk.
Sc. Sciatic nerve trunk, with *I.P.*, internal popliteal, *E.P.*, external popliteal, divisions, and the division going to the hamstring muscles, which gives a cutaneous branch *c'*.
Va.Cr. The vasti and the crureus muscles, the internal portion being especially referred to.

I then attempted to determine if mere tension of the hamstring muscles could give the same result as electrical excitation of the central ends of their nerves. It is, of course, essential that the production of increased tension in the muscles should not alter the

position of the knee joint or affect it mechanically. This precaution was observed by isolating the two inner hamstrings from their attachments, except at their origin, from the *tuber ischii*, and simultaneously cutting through all nerve branches to the outer hamstrings and to the adductor muscles. The nerves to the inner hamstrings were carefully preserved although the muscles were otherwise dissected out. It was found that by pulling on the inner hamstring muscles sufficiently to stretch them out of the doubled-up shape they assumed after being freed from their lower attachments, the knee-jerk, previously brisk, was at once *abolished or greatly diminished*, and on relaxing the strain on the hamstring muscles at once reappeared, and was apparently somewhat more brisk than before the diminution. It is often sufficient to merely compress the hamstring muscles, as they lie flaccid on the hand, between fingers and thumb. A kneading of the muscle as in *massage* has the same effect. On two occasions, at the end of an experiment, when the muscles had suffered from exposure, I have seen the curious phenomenon that excitation of a motor root supplying them of strength insufficient to throw the injured muscles into obvious contraction yet suffices to at once cut out the "knee-jerk," although before and after the excitation the "jerk" was very brisk indeed. The effect was obtained several times in succession, and immediately disappeared on dividing the sensory roots coming in from the exposed muscles. The current of injury in the muscles must have been considerable, and this suggests that the mere negative variation of the current of injury in the muscles might originate centripetal impulses. Certainly there was on neither occasion any obvious contraction in the muscles.

The most efficient mode of excitation of the afferent fibres from these muscles appears to be the mechanical above described, *i.e.*, the *myotatic* (Gowers).*

Excitation of the central end of the divided popliteal or peroneal nerves does not produce this effect upon the jerk. Neither does stretching of the crural triceps by pulling on the tendo Achillis, nor stretching of the rectus femoris muscle. Stretching of the rectus femoris can easily be employed without interference to the movement of the knee joint. It appears to me neither to increase nor to diminish the jerk. Excitation of the central end of the divided nerve to the rectus femoris exerts likewise no obvious influence on the jerk; nor does excitation of the central end of the cutaneous divisions of the anterior crural, viz., the internal saphenous and the internal and middle cutaneous nerves of the thigh. Excitation of the central

* 'Diagnosis of Diseases of the Spinal Cord,' 2nd edit., 1881, p. 29. See also the same author's "Diseases of the Spinal Cord,' vol. i, p. 21; also pp. 202—205, 428, 429, 2nd edit., 1892.

end of the cutaneous branch of the hamstring nerve itself also appears without effect upon the jerk.

Tension produced in the crural triceps muscle by pulling on the Achilles tendon does not appear to influence the brisk flexor movement of the ankle joint evoked by tapping the subcutaneous face of the tibia, and related chiefly to the 6th lumbar spinal segment of *Macacus* and to the 7th lumbar segment of the Cat.

It would thus seem clear that the exaggeration of the knee-jerk produced by severance of the branches given from the great sciatic nerve to the hamstring muscles is not due to the fact that the resulting relaxation of those muscles simply leaves the joint mechanically more free to move. The exaggeration would seem due rather to the severance of the nerves in question interrupting a stream of centripetal impulses that passes up from the hamstring muscles and enters the spinal cord by certain afferent roots, and in the cord exerts a depressing or restraining influence on the jerk. It further appears that a stream of impulses similarly efficient can be set up by moderate electrical excitation of the central ends of the divided nerves of the hamstring muscles; or by simply stretching or kneading those muscles when they are released from one of their fixed points; or, finally, by simply throwing those muscles into contraction through excitation of motor roots supplying them, so long as the sensory roots remain intact. The physician, when he, in order the better to elicit the jerk, flexes the knee and reduces the strain in the flexor muscles, by doing so removes, with relaxation of the flexors, a physiological depression which the tension of those muscles normally exerts upon the jerk obtainable from their antagonistic group.

Further, it would seem that at the knee joint excitation of the afferent fibres coming from one set of the antagonistic muscles induces reflex tonic contraction of the opposing set with extreme facility, despite the fact that the opponent muscles are not innervated from the same spinal segments. The reflex is obtainable with extraordinary facility, even across intervening segments of the cord.

Thus the degree of tension in one muscle of an antagonistic couple intimately affects the degree of "tonus" in its opponent, not only mechanically, but also reflexly, through afferent and efferent channels and the spinal cord.

It is obvious that the correlation of action thus existing between the antagonistic muscular groups of the thigh and knee may be not widely different from that originally pointed out by Hering and Breuer as regulative of the movements of respiration. One is tempted to institute a comparison also between it and the physiological arrangement studied by Biedermann in the antagonism of the muscles of the forceps of *Astacus*. I would, however, reserve further details until I have been able to perform a larger number of

experiments. Anatomical evidence is at present so scanty regarding afferent nerve fibres from muscle that investigation of their anatomical relation seems absolutely requisite for examining the problem further.

[Just as the lumbo-sacral region of the cord may be split along the median plane without interference to the jerk of either side,* so the same may be done without hindering the above ascending reflex abolition of the jerk. Extinction of the jerk by exciting the central end of the 8th root (from hamstrings) affects the jerk four segments higher without in that distance spreading over to the opposite side. But the excitation affects the jerk of the opposite side if the scope of a considerable length of cord be allowed it. If in the Cat the cord be transversely divided at the 11th thoracic segment, excitation of the afferent fibres from a hamstring muscle of one side (*e.g.*, right) applies chiefly to the jerk on the same side (right), but also to the jerk on the opposite. If, however, in the Cat (in which jerk belongs to the 6th and 5th lumbar segments) the cord be transversely cut at or below the 3rd, the extinction from the hamstring nerve is confined to the same side only. In other words, the presence of additional higher segments seems requisite before the passage of the impulses in question across the median plane of the cord, a fact in curious harmony with an observation by Hallstén† regarding the elicitation of "crossed reflexes" in the frog. The median posterior column between the 8th and 4th lumbar levels can be removed *in toto* without impairing the influence of the hamstring nerve on the jerk. It is clear also that those fibres of the posterior root which pass to Clarke's column cannot be the requisite afferents, either from the extensor or flexor thigh muscles, because the jerk and the above-described extinction of it are unaffected in the Cat by transverse section of the cord just below the 4th lumbar segment, *i.e.*, the segment where Clarke's column stops short.—*February* 8, 1893.]

* Sherrington, 'Journ. of Physiol.,' vol. 13, p. 666.
† 'Archiv f. Physiol.,' 1885.

HARRISON AND SONS, PRINTERS IN ORDINARY TO HER MAJESTY, ST. MARTIN'S LANE.